

## Population demography and seed bank dynamics of the threatened obligate seeding shrub *Grevillea maxwellii* McGill (Proteaceae)

S Barrett<sup>1</sup> & A Cochrane<sup>2</sup>

<sup>1</sup> Department of Environment and Conservation  
120 Albany Highway, Albany WA 6330  
✉ sarah.barrett@dec.wa.gov.au

<sup>2</sup> Department of Environment and Conservation,  
Locked Bag 104, Bentley Delivery Centre, WA 6983

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### Abstract

*Grevillea maxwellii* McGill (Proteaceae) is a threatened endemic perennial shrub restricted to the Pallinup River corridor in southern Western Australia. This obligate seeding species was demonstrated to have a low fruit to flower ratio (0.0123) and a small soil-stored seed reserve of 24.4 m<sup>-2</sup> that remains highly viable (greater than 90 %) for at least 12 months. After disturbance the seedling to parent ratio was 9:1, and the juvenile period for this species was at least four years. Fire and episodic autumn rainfall events appeared to provide the most effective stimuli for recruitment however seedling survival was adversely affected by grazing and drought. Over the study period survival of the largest cohorts of seedlings ranged from 5.3% (after fire treatment) to 8.7% (no disturbance). Percentage mortality of adult plants ranged from 30% to 37% pre-study to 9% to 12% during the study. Inter-fire recruitment was effective in maintaining population stability over the four-year study period however small population size renders this threatened species vulnerable to stochastic environmental events. Too frequent disturbance in combination with low seed production, juvenile period, drought and grazing have the potential to drive this species to extinction.

**Keywords:** *Grevillea*, fire, germination, conservation, seed production, recruitment, survival, threatened species.

### Introduction

Episodic and event dependant recruitment (fire, rainfall, mechanical disturbance) is common in fire-prone ecosystems and has been shown in a range of *Grevillea* species from Australia (e.g., Auld 1995, Auld & Tozer 1995, Auld & Scott 1996, Vaughton 1998, Kenny 2000, Morris 2000, Pickup *et al.* 2003). Germination can be triggered by disturbance that alters the environment around the seed making it favourable for seedling establishment and/or altering the dormancy state of the soil-stored seed reserve (Fenner & Thompson 2005). A species' response to disturbance is determined by life-history attributes such as seed characteristics, seed storage and dispersal, seed availability, and the ability for seedling recruitment and persistence (Noble & Slatyer 1980). For successful regeneration after disturbance, the interval between disturbances must be long enough to allow seedlings to mature and replenish the seed bank, but not so long that seed or adult longevity is exceeded. This juvenile period is a critical stage in the life cycle of the plant. For long-lived woody perennials too frequent disturbance events may increase the risk of local population extinction, particularly if the disturbance occurs during the juvenile period, if annual seed production is low and predation rates are high, or if disturbance events stimulate germination and exhaust the soil-stored seed reserve (Auld 1995; Keith 1996;

Regan *et al.* 2003; Auld & Scott 2004). The risk of extinction increases if subsequent seedling survival is low due to drought and grazing.

For obligate seeding species the seed bank strongly influences population dynamics and persistence after disturbance events. Low seed bank size may be due to low fecundity, pre- and post-dispersal seed losses, low seed viability and low seed longevity in the soil. For species with restricted distributions the seed bank size may contribute to rarity. Members of the Proteaceae often have extremely low fruit to flower ratios (0.001–0.163) (Collins & Rebelo 1987), a phenomenon particularly apparent in the genus *Grevillea* (Table 1). Naturally low fruit to flower ratios are a result of interacting factors including pollen and resource limitation, and fruit predation (Stephenson 1981). In many cases, plants adopt a bet hedging strategy where excess flowers help match seed production to resource availability in low resource habitats. This attracts pollinators and ensures fruit set with high pre-dispersal predation (Ehrlén 1993).

Two hundred and twenty-five of the 357 Australian *Grevillea* species (Makinson 2000) occur in Western Australia. The genus is the third largest in the State after *Acacia* (587) and *Eucalyptus* (391) (<http://florabase.calm.wa.gov.au/statistics>). *Grevillea* species are found throughout all habitats and ecosystems, displaying a variety of forms and life history attributes. Western Australia has 112 listed threatened species and subspecies in this genus (Atkins 2006). The endemic

Table 1

Habitat, reproductive mode and fruit to flower ratio (FR: FL) in *Grevillea* species.

Species	Habitat	Seeder (S) Resprouter (R)	FR: FL ratio	Citation
<i>G. althoferorum</i>	SW WA sandplain	R	0.0015	Burne <i>et al.</i> 2003
<i>G. barklyana</i>	VIC riverine	S	0.019, 0.001–0.053	Vaughton 1995, 1998
<i>G. beadleana</i>	NE NSW riverine	S	0.007 – 0.100	Smith and Gross 2002
<i>G. caleyi</i>	NSW woodland/heath	S	0.0300	(cited in Vaughton 1998)
<i>G. humifusa</i>	SW WA woodland/heath	S/R	0.0900	Harris & Yates 2003
<i>G. leucopteris</i>	SW WA open heath/tall shrubland	S	0.0530	Lamont 1982
<i>G. linearifolia</i>	E NSW woodland	S	0.0150	Hermanutz <i>et al.</i> 1998
<i>G. longifolia</i>	NSW sclerophyll forest	S	0.0380	Hermanutz <i>et al.</i> 1998
<i>G. maxwellii</i>	SW WA low heath	S	0.0123	Present study
<i>G. mucronulata</i>	E NSW sclerophyll forest	S	0.0320	Hermanutz <i>et al.</i> 1998
<i>G. oleoides</i>	S NSW open heath/woodland	S/R	0.0960	Hermanutz <i>et al.</i> 1998
<i>G. rudis</i>	SW WA shrubland	S	0.0027	Burne <i>et al.</i> 2003
<i>G. sphacelata</i>	Coastal NSW heath /dry sclerophyll woodland	R	0.0260	Hermanutz <i>et al.</i> 1998
<i>G. synapheae</i>	SW WA heath/woodland/shrubland	S	0.0037	Burne <i>et al.</i> 2003
<i>G. wilsonii</i>	SW WA forest/woodland	S/R	0.0640	(cited in Vaughton 1998)

Western Australian *Grevillea maxwellii* (McGill) is ranked as endangered under the Australian Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (<http://www.deh.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=flora>) and meets the World Conservation Union (IUCN 2001) Red List Category 'CR' under criteria B1+2ce. Although *G. maxwellii* is endangered and has an Interim Recovery Plan (Phillimore *et al.* 2001), there is no published information on the ecology or biology of the species. Basic census data on abundance is gathered on a regular basis and seedlings have been observed at one population, but their contribution to population stability and persistence is unknown (S. Barrett, unpublished data).

This study investigates some key life history attributes that affect the population dynamics of *Grevillea maxwellii*. We examined population structure, quantified fruit to flower ratio, assessed the magnitude, viability and disturbance response of the soil-stored seed reserve, and determined the factors that affect seedling survival in order to contribute to the management and long-term conservation of the species.

## Materials and methods

### Study species

*Grevillea maxwellii* is a small, spreading spring-flowering shrub with lobed leaves and large red inflorescences which shelter beneath the foliage (Olde & Marriott 1995). The species is related to *G. asparagoides*, *G. batrachioides* and *G. secunda*. *G. maxwellii* grows in low open heath in shallow brown loamy soil over granite on rocky hilltops and slopes to the Pallinup River east of the Stirling Range in the South West of Western Australia. Plants become rarer as the soil depth increases (Robinson & Coates 1995). The species may be pollinated by nectarivorous birds (Olde & Marriott 1995), although mammal pollination has also been suggested (Obbens 1997). The glandular brown fruits mature over two to three months and contain one ellipsoidal seed c. 9.35 x

3.95 mm in size, with a mean weight of 0.04 g (n = 20). Seeds of *G. maxwellii*, like that of other *Grevillea* species, are released annually. They have no clear dispersal mechanisms, although a narrow waxy wing around the edge of the seed may be attractive to ants. Under controlled conditions dormancy of fresh seeds is broken when the seed coat is damaged by scarification. Smoke application has been found to be beneficial in stimulating germination (A. Cochrane unpublished data). The response of the species to fire has not been studied previously but like many other *Grevillea* species, *G. maxwellii* is considered to be an obligate re-seeder killed by fire with a soil-stored seed bank (Olde & Marriott 1995).

*G. maxwellii* was originally collected by the explorer and botanist James Drummond in 1840. Another collection was made in 1966 and again in 1986 when the species was known from one population of over 40 plants. With extensive survey in recent years, the species is now known from nine fragmented populations containing less than 1000 plants (pers. comm. S. Barrett). The main threats to the survival of the species are drought and inappropriate fire regimes. At the commencement of the present study all of the nine known populations were long unburnt and considered to be senescing and facing gradual and ongoing decline.

### Study sites

Two study sites were chosen east of the Stirling Range National Park and southwest of the Pallinup River. The climate of the area is dry Mediterranean with cool wet winters; hot, dry summers and a mean annual rainfall of 420.5 mm per annum (1968–2006). Mean monthly maximum rainfall of 48.4 mm occurs in July and the mean monthly minimum of 19.1 mm occurs in February. Both sites were determined to be long unburnt (more than 25 years since last fire) based on local knowledge. The response of *G. maxwellii* to disturbance was studied at Site 1 (Unallocated Crown Land (UCL), 34° 16' S 118° 26' E) where the longevity of the soil seed bank and fruit to flower ratio were also examined. Just over 100 mature plants occur at this site. The vegetation is low heath on shallow sandy loam over granite. Associated species

include *Allocasuarina campestris*, *Calothamnus quadrifidus*, *Hakea marginata*, *Gastrolobium spinosum*, *Melaleuca hamata*, *Calytrix tetragona* and *Borya sphaerocephala*. The second site, where seedling survival in the absence of disturbance was studied, was on private property (34° 18' S 118° 30' E) where approximately 50 mature plants were located in open *Allocasuarina huegeliana* woodland over low open heath with *Hypocalymma angustifolium*, *Calothamnus quadrifidus*, *Hakea lissocarpa*, *Stypantra glauca* and *Borya sphaerocephala*. Soils here are generally shallower than those of Site 1 with a greater percentage cover of bare rock. Monthly rainfall data was obtained from adjacent property owners for the duration of the study period.

### Life history and population structure

At the commencement of the study in 2001/2002 and again in 2006, the size and structure of each population was determined by walking transects through the population. Plants were allocated to one of four age classes: living large mature (canopy area > 0.5 x 0.5 m), young mature (canopy area < 0.5 x 0.5 m, > 0.2 x 0.2 m), and juvenile plants (< 0.2 x 0.2 m) and dead plants. As growth of mature plants was primarily horizontal with little vertical growth, plant height was not considered to be a useful indicator of age. Young seedlings at the cotyledon stage were not recorded in these transects.

### Seed production

Seed production was examined at Site 1 over one flowering season in 2004. Three stem sections were sampled on each of 10 randomly selected mature plants in 2 m x 2 m quadrats established to monitor the effect of disturbance. Stem sections were approximately 10 cm in length. At the commencement of the reproductive phase the total number of inflorescence buds in each section was counted. In November 2004, the total number of mature fruit was then recorded. Fruit set for *G. maxwellii* was compared with that of other *Grevillea* species documented in the literature (Table 1).

### Soil Seed Bank

To investigate the distribution and magnitude of the soil seed bank a total of 40 soil samples (15 cm x 15 cm x 20 mm) were collected from beneath the canopy of 20 randomly selected plants (10 live and 10 dead) at each site. Samples were air dried and passed through a series of different sized sieves. Gravel and larger rocks and litter were fractioned off, removed and soil aggregations broken up until two fractions remained above and below the normal size range of *G. maxwellii* seeds. The fraction below the size range was discarded; the remaining fraction was examined for *G. maxwellii* seeds. The viability of seeds retrieved from the soil-stored seed bank was assessed under conditions that have been implicated in the stimulation of germination of other *Grevillea* species (e.g., Dixon *et al.* 1995; Kenny 2000, Morris 2000; Morris *et al.* 2000; Pickup *et al.* 2003). Seeds were pre-treated with smoked water for 2 hours, rinsed, then manually scarified along the longitudinal axis with a sharp scalpel knife and placed on a 1% w/v agar solution in 9 mm glass petrie dishes. Seeds were incubated at 15°C with 12 hours of alternating light and darkness. Germination was determined as the emergence of the radicle from the seed coat.

### Soil seed longevity

To investigate the longevity of the soil-stored seed bank, a seed burial retrieval experiment was conducted at Site 1. Seeds were collected in late spring 2004 and divided into 20 lots of 10 seeds. Each seed lot was placed into a 10 x 10 cm free-draining nylon mesh bag filled with 50 grams of coarse river sand and sealed. In November 2004, a 3 x 3 m grid was marked with wooden pegs at four points. Bags were randomly selected and five bags buried 5 cm deep at each of the four points. These points were assigned to treatment by burial for 3, 6, 9 or 12 months. On retrieval at the end of the designated period, the five bags were assessed for numbers of decayed, germinated and intact seeds. Intact seeds were assumed viable and assessed for germination under controlled conditions as previously described.

### Seedling emergence and survival in response to fire, smoke and raking

In May 2001, a limited number of 2 m x 2 m study quadrats were established at Site 1 to determine the effect of disturbance (fire, smoke application, raking and no disturbance) on seedling emergence and survival. Each of the 35 quadrats was centred on a single large mature plant of *G. maxwellii*. Five live and five dead plants were used in each of a control and two treatments (smoke and raking); five dead plants were used for the fire treatment with no live plants burnt. The minimum impact design for the disturbance experiment (that is, no live plants burnt) was adopted as a precaution due to the threatened nature of *G. maxwellii*. The canopy size (width of the canopy at the widest point and at 90° to the widest point) of each plant in the 35 experimental quadrats was measured prior to treatment. The mean canopy area of the plants assessed for each treatment was 1.03 ± 0.2 m<sup>2</sup> (fire), 0.8 ± 0.2 m<sup>2</sup> (smoke), 1.06 ± 0.2 m<sup>2</sup> (rake) and 1.1 ± 0.2 m<sup>2</sup> (control). In May 2001 five quadrats were subjected to a moderately hot autumn burn for roughly five minutes per quadrat. Prior to ignition an area of approximately 1 m around each quadrat was raked free of litter and plants to minimise the encroachment of fire on the surrounding bushland. Six ignition points were lit per quadrat. Each quadrat was assessed to have sustained between 95 – 99 % burn with flame heights varying between 0.5 m and 1.5 m high. Ten quadrats (five dead and five live plants) were treated with an aqueous smoke solution (Regen 2000®) at 100 ml m<sup>-2</sup>. Smoke treated quadrats were pre-treated with a soil wetter (Wettasoil<sup>HC</sup> by Garden King) at 5 ml m<sup>-2</sup> to ensure even penetration of the smoke solution. Ten quadrats (five dead and five live plants) were hand raked to bare mineral soil using a rake hoe. Controls were left untreated. Seedling emergence was recorded in spring 2002 and biannually thereafter until winter 2006. All germinated seedlings in 2002 and subsequent years were tagged, numbered and plant growth measured annually. In the burnt quadrats, the mean seedling to parent ratio in the first spring after fire was calculated and the time to first flowering (primary juvenile period) recorded.

### Natural seedling emergence and survival

In November 2001, five 5 m x 5 m quadrats were established at Site 2 where seedlings had germinated apparently in response to the unusually high summer rainfall of January 2000. Quadrats contained recently or

long dead plants with the exception of quadrats 1 and 2 which each contained two live plants. Each seedling was identified with a metal tag, numbered and measured. Quadrats were monitored biannually until winter 2006. New seedlings in subsequent years were also tagged and numbered. Herbivore exclusion cages were erected around approximately half of all seedlings that emerged in August 2003 to determine the effect of grazing on seedling growth and survival. Plant growth and survival was recorded annually and the primary juvenile period recorded.

#### Data analysis

Seed production was estimated as the product of the number of inflorescent buds divided by the proportion of maturing fruit. From this data the percentage fruit set was calculated. Germination level has been expressed as a percentage of the number of intact seeds germinated. Time to first germination was recorded in days. Non-normal data were analysed using a non-parametric Kruskal-Wallis test to compare the percentage survival of fire-recruited seedlings at Site 1 to that of non-fire related recruitment at Site 2 (Statistica for Windows 1995. Statsoft Inc: Oklahoma).

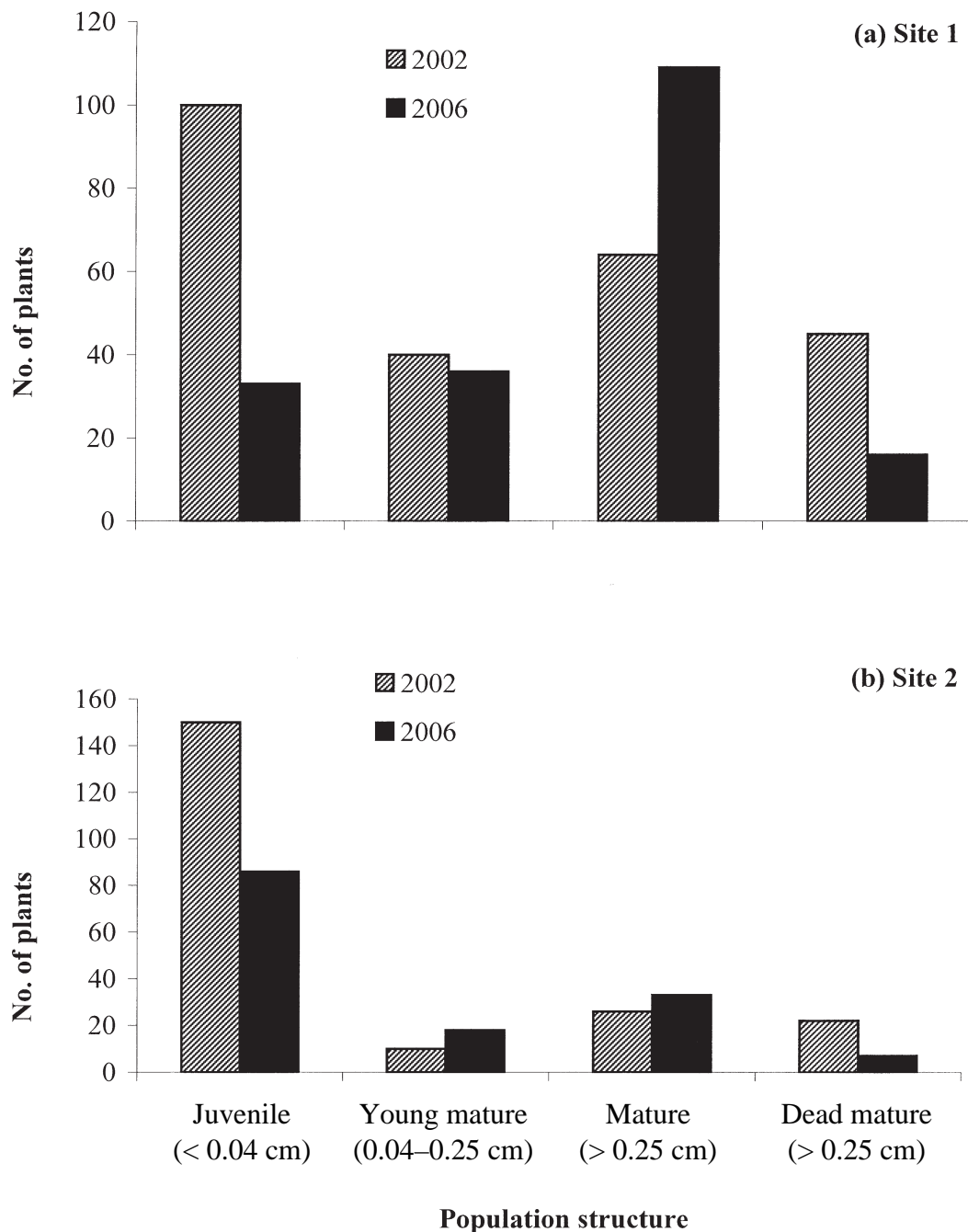


Figure 1. Population structure of *Grevillea maxwellii* at (a) Site 1 and (b) Site 2 in 2002 and 2006.

## Results

### Population structure

At the beginning of the study, the population structure at both sites showed a bimodal distribution with more large mature and juveniles plants and relatively few young mature plants present (Fig. 1a and 1b). Percentage mortality of mature plants was high with 30.2% of mature plants dead at Site 1 and 37.9 % dead at Site 2. At the end of the study both populations had increased in size with a 39.4 % increase in all mature plants at Site 1 and a 41.7 % increase at Site 2, while percentage mortality was 9.9 % and 12.1% at Site 1 and Site 2, respectively.

### Fruit to flower ratio

A mean fruit to flower ratio of 0.0123 was recorded over one season at Site 1. High levels of fruit abortion were observed on all plants as well as high levels of seed predation.

### Soil Seed bank

A total of 22 whole seeds were recovered from 40 soil samples at Site 1 giving a mean seed density of  $24.4 \pm 17.1$  seeds  $m^{-2}$ . The soil stored seed reserve was not distributed evenly with four seed found beneath two live plants and 18 seed found beneath two dead plants. No seeds were retrieved from beneath plants at Site 2. A few samples contained seed fragments and shrivelled seeds indicating that a proportion of the seed crop was either predated and/or aborted. Full germination was attained for all retrieved soil-stored seeds. First germination commenced at 10 days with final germination achieved after 44 days (Fig. 2).

### Soil seed longevity

A high proportion of seeds remained intact over the 12-month period of the experiment and ranged from 80 % after nine month's burial to 90 % after 12 month's

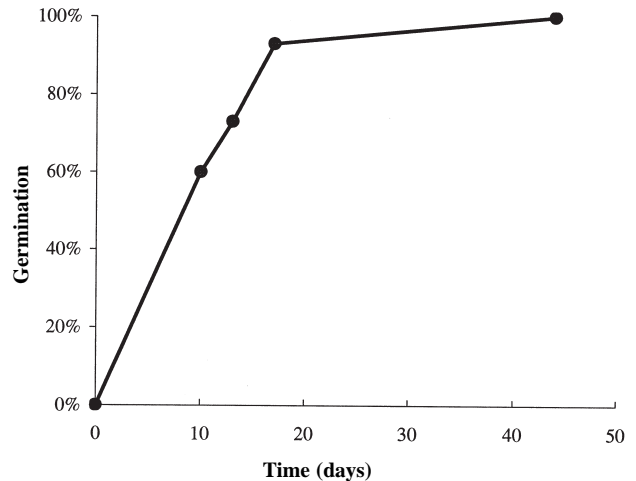


Figure 2. Percent germination over time in days of seeds retrieved from the soil seed bank of *Grevillea maxwellii* at Site 1.

burial (Table 2). Similarly, percentage germination of retrieved seeds remained high from the first retrieval at three months to the last retrieval after one year with the exception of the nine-month retrieval where percentage germination dropped to 65 %. Time to first germination for soil-stored seeds ranged from 11 to 15 days.

### Germination response and plant survival with and without disturbance

Total seedling emergence over the study period at Site 1 in 2  $m^2$  plots varied with treatment and ranged from six seedlings (no treatment) to 48 seedlings (fire treatment). Fire resulted in the greatest germination response with the highest seedling density of 1.9  $m^{-2}$  recorded the first spring after the autumn burn at Site 1 (Table 3). There was a mean seedling to parent ratio of 9:1 in burnt quadrats. Germination continued the

Table 2

Percentage of *Grevillea maxwellii* seeds remaining intact after burial for 3, 6, 9 and 12 months at Site 1 and their percentage germination after pre-treatment with smoked water and manual scarification. N = 50 seeds retrieved at each time period.

Retrieval time in months	Percent seed remaining intact after burial	Percent germination of intact retrieved seeds	Time to first germination in days
3	$86 \pm 0.04$	$95 \pm 0.05$	11
6	$82 \pm 0.08$	$90 \pm 0.08$	15
9	$80 \pm 0.05$	$65 \pm 0.10$	15
12	$90 \pm 0.08$	$90 \pm 0.04$	14

Table 3

Mean density of seedlings ( $m^{-2}$ ) recorded annually (not cumulative) in quadrats with disturbance (Site 1 only) and without disturbance (Site 1 and Site 2).

	Fire	Smoke	Rake	Natural (Site 1)	Natural (Site 2)
2000/2001	n/a	n/a	n/a	n/a	$0.92 \pm 0.19$
2002	$1.90 \pm 0.17$	$0.13 \pm 0.04$	$0.00 \pm 0.00$	0.00	$0.04 \pm 0.01$
2003	$0.25 \pm 0.10$	$0.10 \pm 0.06$	$0.03 \pm 0.03$	0.00	$0.23 \pm 0.13$
2004	0.00	0.00	0.00	0.00	$0.02 \pm 0.02$
2005	$0.25 \pm 0.08$	$0.18 \pm 0.08$	$0.35 \pm 0.13$	$0.15 \pm 0.08$	$1.00 \pm 0.43$

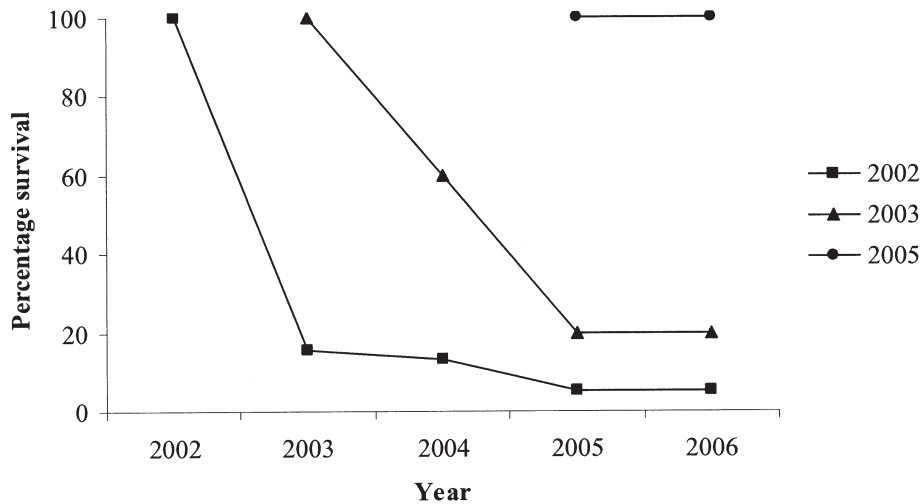
subsequent and fourth year in the burnt quadrats but at much lower densities of 0.25 seedlings m<sup>-2</sup>. There were very low levels of recruitment in response to smoked water and raking from 2002 to 2004. However, there was significant germination in 2005 in the raked quadrats. There was no natural recruitment recorded within control quadrats at Site 1 from 2002 to 2004 although low levels of germination were noted throughout the population. In contrast, high levels of germination were recorded at Site 2 (no disturbance) in 2001 and 2005, resulting in the next highest seedling densities recorded during the study of 0.9 m<sup>-2</sup> and 1 m<sup>-2</sup>, respectively. Total seedling emergence over five 5 m<sup>2</sup> plots at Site 2 for the study period was 276.

The overall survival of fire-recruited seedlings at Site 1 was low, with a mean survival of only 5.3 % in 2006 for the largest (2002) cohort (Fig. 3a). There was a higher percentage survival at Site 2 compared with Site 1 with

8.7 % of the largest (2000/2001) cohort surviving in 2006, however this difference was not statistically significant. By 2006, there were no survivors of 2002, 2003 and 2004 cohorts at Site 2 with steep increases in mortality recorded in the early years after germination (Fig. 3b).

Survival of seedlings over the first summer ranged from 15.8 % in 2003 to 100 % in 2006 at Site 1, and from 46.1 % in 2002 to 68.8 % in 2006 at Site 2. In the first summer after germination, 86.7 % of live and 39.1 % of dead seedlings of the 2002 (fire) cohort showed signs of grazing at Site 1. In contrast, only 7 % of the 2005 cohort (including raked, smoked and control quadrats) showed evidence of grazing. At Site 2, 36.4 % of live and 27.7 % of dead plants were grazed in the summer of 2002. As for Site 1, there was minimal grazing of the 2005 cohort in the summer of 2006. Of the 14 germinated seedlings of the 2003 cohort that were caged at Site 2 in August 2003, 12 were alive in summer 2004 while nine of 12 non-caged

(a) Site 1



(b) Site 2

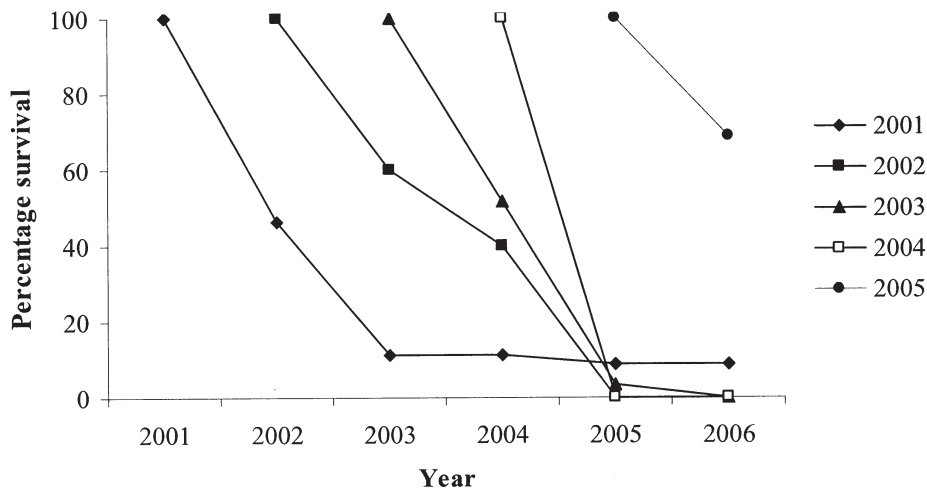


Figure 3. Percentage survival of successive cohorts of seedlings germinated over 4–5 years at (a) Site 1 (fire disturbance only); (b) Site 2.

plants survived. Mean plant height doubled from 2.5 cm to 5.0 cm for caged plants and by 2.0 cm from 2.4 cm to 4.4 cm for non-caged plants. However, by 2006, all of the caged and non-caged plants had died. Overall survival of all seedlings recorded over the study period, excluding the 2005 cohort, was 5.7 % at Site 1 and 6.6 % at Site 2.

The mean annual rainfall for the study period 2000 to 2006 was 411.9 mm, marginally less than the long term average of 420.5 mm (1968–2006). Below-average rainfall occurred in 2000, 2002, and 2004, with above-average rainfall in the three other years, with some significant peaks in rainfall in December 2001 (113 mm), August 2003 (133 mm) and March 2005 (147 mm). Over the study period, germination of *G. maxwellii* was observed primarily in the months of May and June and significant germination followed high rainfall between March and May 2005 (280 mm in total). The high rainfall events of December 2001 or August 2003 did not promote germination.

### Juvenile Period

At Site 1, one of the two plants surviving of the 2002 cohort flowered in winter 2006, four years after germination. At Site 2, six of 13 surviving plants flowered in 2004, four years after germination. This suggests a juvenile period of at least four years for *G. maxwellii*. Mean plant height at that time was  $21.0 \pm 2.0$  cm and mean canopy dimensions were  $44.3 \pm 6.1 \times 30.3 \pm 5.2$  cm. All of 10 surviving plants (8.9 % of the 2000 cohort) were reproductive in 2006, six years after germination.

## Discussion

Successful recruitment and survival of perennial shrubs may be dependant on their reproductive biology, establishment ecology or a combination of both (Yates & Ladd 2004). Population stability relies on a balance between recruitment and mortality. In the present study, high levels of adult mortality of *Grevillea maxwellii* (30.2 to 37.9 %) were recorded at the onset in long unburnt (> 25 years) populations and this was suggestive of drought-induced mortality, death through senescence or a combination of both. Similarly, high levels of mortality and senescence were recorded for the rare re-seeder *G. barklyana* in a 29-year-old population (Vaughton 1998). Mortality of adult plants of re-seeder species may increase with time since fire and may be exacerbated by drought (Vaughton 1998). High levels of adult mortality have also been recorded for *G. calyei* in relation to fire history (Auld & Scott 2004). While significant numbers of small juvenile plants were observed at the onset of the present study it appeared that few of these survived to become young adults. However, by the end of the study both populations had effectively increased in size indicating that a proportion of juveniles were indeed successful in reaching maturity and that the seed bank continued to contribute to population dynamics either with or without disturbance stimuli.

Members of the Proteaceae have extremely low mature fruit to flower ratios compared to other temperate, hermaphroditic woody perennials (Collins & Rebelo 1987). Low fruit to flower ratios in *Grevillea* result from a combination of pollen limitation and high levels of flower and fruit predation (Hermanutz *et al.* 1998). The fruit to

flower ratio of 0.0123 recorded in the present study was consistent with those of other members of the genus where ratios ranged from a minimum of 0.001 for *G. barklyana* (Vaughton 1998) to a maximum of 0.09 recorded for *G. oleoides* (Hermanutz *et al.* 1998). Low fruit to flower ratio in *G. maxwellii* may have resulted from high levels of abortion or inefficient pollination as well as pre-dispersal predation by insects and birds. The fragmented nature of *G. maxwellii* populations may influence the abundance and effectiveness of pollinators and therefore levels of abortion, but specific pollination studies would be required to confirm this. As no bird pollinators were observed over the study period, mammals are the more probable vectors.

Despite low annual seed production, *G. maxwellii* maintained a small highly viable but very patchy soil-stored seed reserve at one site. Edwards & Whelan (1995) also reported the presence of a small soil-stored seed bank for the re-seeder *G. barklyana*, with mean seed densities estimated at between 4.3 – 14.1 seeds m<sup>-2</sup> from under-canopy samples. Seed bank size was related to time since fire and no seeds were retrieved from outside the canopy area of the plants studied. Although these seed densities are somewhat smaller than those reported during the present study for Site 1 (24.4 seeds m<sup>-2</sup>), there was considerable variation between samples and many had no seed at all which is comparable with our results for *G. maxwellii*. Seed bank densities from 0 to 30 seeds m<sup>-2</sup> were recorded for the re-seeder *G. rudis* while no seed bank was detected for the rare resprouter, *G. althoferorum* (Burne *et al.* 2003). In contrast, soil seed bank density in the present study was considerably lower than that recorded for *G. rivularis* (194 seeds m<sup>-2</sup>) a species which occupies habitat subject to periodic disturbance from both fire and flood (Pickup *et al.* 2003).

Data from the seed burial experiment indicates that the soil seed bank of *G. maxwellii* persists in a highly viable state for at least one year. The seed bank of the rare *G. calyei* was estimated to have a half-life of 7.6 years (Auld *et al.* 2000) remaining in the soil for many years after the death of adult plants. Recruitment of *G. maxwellii* seedlings under dead plants suggests seeds may also remain viable in the soil for several years after the parent plant dies and are available for recruitment when an appropriate stimulus is provided. Unfortunately, there is little in the literature regarding the ability of species with soil seed banks to maintain a seed bank after fire (Auld & Denham 2006). The ability to maintain a soil-stored seed bank may buffer the impact of high frequency fires. If some residual seeds remains in the soil there will be some risk spreading at least in the short-term, providing species with a second chance at recruitment. The present study showed that although the density of seedlings was considerably lower in the second and fourth years after fire, a small viable seed bank had persisted over time. The persistence of a soil seed bank after fire has also been reported for the threatened Proteaceous species *Persoonia micranthera* and the weakly serotinous *Dryandra ionthocarpa* subsp. *ionthocarpa* (Barrett unpublished data). The persistence of a residual soil seed bank may be related to depth of soil burial. Where seed dormancy in *Grevillea* species is broken by a combination of smoke and heat shock it has been suggested that the smoke cue may decline with soil depth (Auld & Denham 2006).

Despite the establishment of few plots and restricted treatments in accordance with a minimal impact design experiment for threatened species, fire at Site 1 provided the most successful experimental disturbance stimulus for seedling emergence of *G. maxwellii*. Fire regimes play an important part in the ecology and survival of many plant species in fire-prone environments. Recruitment is frequently linked to fire and obligate seeding species are often dependent on recruitment after fire or other disturbance for persistence in the landscape. Heat associated with fires is an important mechanism for releasing dormancy (Fenner & Thompson 2005) and the role of heat in the induction of seed germination of many Western Australia fire-following plant species is well documented (for example see Bell *et al.* 1993; Bell 1999). Heat acts to fracture the seed coat of hard-seeded and other species (Bewley & Black 1994). Smoke has also been shown to increase stimulation of germination in species from Mediterranean fire-prone environments (for example see Brown & van Staden 1997; Keeley & Fotheringham 1998; Roche *et al.* 1998), although Bell (1999) noted that a number of studies reported that smoke-induced seed germination was less successful than heat in the induction of germination. In the present study, the results indicate that smoke treatment did not stimulate germination of the soil-stored seed to the same degree as heat from fire, and few seedlings emerged in quadrats treated with smoke and none of these survived summer drought conditions. Similarly, there was little recruitment in direct response to raking. Although smoke treatment was used in the laboratory to stimulate germination of fresh and aged seeds, no seeds were germinated under non-smoke treated conditions for comparison due to a lack of available seeds. However, significant germination in the absence of disturbance was observed in 2001 and 2005. Recruitment in 2005 in particular appears to have been triggered by high rainfall in March of that year. While fire-related germination cues are most common in the genus *Grevillea* (Kenny 2000, Morris 2000), episodic recruitment after disturbance other than fire has been reported in a number of species including *G. longifolia* (Auld 1995), *G. buxifolia* and *G. speciosa* (Auld & Tozer 1995), *G. caleyi* (Auld & Scott 1996), *G. macleayana* (Vaughton 1998) and *G. rivularis* (Pickup *et al.* 2003). Seedling recruitment in *G. rivularis* has been recorded after fire, flood and mechanical disturbance with seeds showing marked dormancy polymorphism with 36 % of soil-stored seeds germinating without treatment. Thus the species can respond to disturbance by fire or flood. The results of the present study clearly indicate that seeds of *G. maxwellii* can also respond to non-fire related cues such as the episodic rainfall events previously described and we suggest that seeds may be polymorphic. Polymorphism has been reported also for *G. barklyana* (Edwards & Whelan 1995) who suggest that decreased dependence on fire as a means of germination stimulation may be associated with increased fire interval. Seed age and weathering over time may play a role also in a recruitment event with wetting and drying cycles over summer and autumn contributing to the release of any seed dormancy. It is possible that summer rainfall events may have depleted the seed bank at Site 2 through recent recruitment, thus accounting for lack of a discernable soil-stored seed reserve.

The seedling to parent ratio of 9:1 and seedling density of 1.9 m<sup>-2</sup> recorded in the present study for *G. maxwellii* is lower than that of 20:1 and 4.6 m<sup>-2</sup>, respectively, recorded for *G. barklyana* (Vaughton 1998). However, recruitment in the latter species was negligible in the absence of fire and this species is likely to be more fire-responsive than *G. maxwellii*. Furthermore, only dead plants were burnt in the present study, and there may have been greater recruitment from burning living plants.

High levels of seedling mortality were a feature of both sites in the present study. Early seedling mortality is a widespread occurrence in woody plants (Harper 1977). Lack of adequate moisture is often a controlling factor that limits survival, and where seedling densities are high, mortality can increase (Clarke 2002). Survival curves for seedlings of semi-arid shrubs are approximately 1 % (Clarke 2002). Survival of the two major cohorts followed in the study ranged from 5.3 to 8.7 % and overall 5.7 % and 6.6 % of all germinated seedlings survived at Site 1 and Site 2, respectively. In contrast, 90 % survival was recorded for fire-recruited seedlings of *G. barklyana* over a 2-year period (Vaughton 1998). However, the latter study coincided with two years of above average rainfall demonstrating the importance of adequate soil moisture for seedling survival. In contrast, the 2002 rainfall in the present study was 130 mm below the average which would have had a significant impact on post-fire establishment and seedling survival. Grazing can also have a profound effect on seedling survival (Clarke 2002) and loss of seedlings at both sites in the present study was partially attributed to herbivore grazing. Defoliation of many seedlings resulted in suppressed growth, possibly increasing the juvenile period. The prime factor that contributed to low seedling survival after recruitment is not clear. Herbivore grazing or drought conditions or a combination of these factors may have been responsible. However, drought was probably the more significant factor in seedling mortality as several seemingly dead and grazed seedlings recovered following winter rains while no caged seedlings survived the study period. Grazing was largely restricted to the summer period with little or no grazing noted over winter and spring. The major decline in seedling numbers occurred during summer and seedling death during this time is attributed to below average rainfall following recruitment. At Site 1, 86.7 % of live and 39.1 % of recently dead, fire-recruited seedlings exhibited signs of grazing. This was considerably higher than at Site 2 where 36.4 % of live and 27.7 % of dead plants had been grazed in unburnt vegetation.

Seedling recruitment between fires may be strongly related to the availability of competition-free sites in addition to rainfall (Yates & Ladd 2004), and the relatively high level of recruitment in the raked quadrats in 2005 suggests that germination of *G. maxwellii* under adequate soil moisture conditions may also be dependent on the presence of adequate gaps in the canopy.

While flowering commenced in the present study at four years after germination, peak flower and fruit production may take many more years. Flowering of *G. barklyana* occurs after 2 to 3 years, although maximum inflorescence and fruit production did not occur until 15–



16 years after fire when plants reached full size but declined thereafter (Vaughton 1998). The juvenile periods of other obligate seeding *Grevillea* species (*G. caleyi* and *G. longifolia*) (Vaughton 1998) are comparable to that of *G. maxwellii*, although in contrast, *G. wickhamii* had not flowered four years post-fire and only one third of *G. dryandri* plants had flowered after three years (Williams *et al.* 2006).

## Conclusions

Although constrained by a limited number of plots and treatments in accordance with a minimum impact design experiment, this study has provided a temporal insight into the ecology and population demography of *G. maxwellii*. We have identified that the two populations studied are not in decline, at least in the short term. However, the long term success of the inter-fire recruitment documented in the present study is unclear. This study suggests that factors associated with the availability of the regeneration niche may be more important than reproductive factors, and population persistence may be more related to stochastic environmental events (Yates & Ladd 2004). Small fragmented populations of *G. maxwellii* are highly vulnerable to stochastic events such as wildfire followed by drought conditions. Climate change may increase the risk of wild-fire and create adverse conditions for seedling survival potentially causing local extinctions of *G. maxwellii*.

While it is possible that summer rainfall events may become more frequent in the south-west of Western Australia (CSIRO 2001), the overall projected decline in annual rainfall may limit the numbers of seedlings that survive to maturity. There may be some risk spreading through the maintenance of a residual seed reserve but recruitment will be dependent on the magnitude of the germination cues as well as the location of seeds in the soil profile (Auld & Denham 2006). Infrequent disturbance can also cause local extinction, particularly in small isolated fragments as adult plants senesce (Keith 1996; Yates & Ladd 2004). The soil seed bank may buffer loss of genetic diversity in small populations through i) its ability to increase effective population size to well above that of the adult plants, ii) by the longevity of the seed bank enabling storage of genetic diversity long after adult plants have died and iii) through the presence of multiple generations of seeds in the seed bank due to some remaining after fire (Llorens 2003). However, the seed bank buffering powers may be limited and are unlikely to prevent the loss of genetic diversity in populations that remain small over several generations causing inbred individuals that may have lower fitness (Llorens 2003).

Future investigations aimed at quantifying predation and removal rates of *G. maxwellii* seeds would provide useful data to assist in understanding the relationship between seed production, soil seed bank size and recruitment. Quantification of the soil-stored seed reserve over time would permit a greater insight into the dynamics of the seed bank. Population modelling may assist in predicting population dynamics over a range of environmental conditions however the soil-stored seed reserve needs to be considered in estimates of population

abundance where there is a high level of senescence and death of above-ground plants (Auld & Scott 2004). It is critical that *G. maxwellii* populations are managed to ensure that entire populations and / or multiple populations do not burn in a single wild-fire event. Controlled burns targeting small portions of these long unburnt populations may reduce the impact of potentially high post-fire seedling mortality. With anticipated warming climates, the future persistence of *G. maxwellii* in the wild is in doubt. Little can be done to counter the effects of a warming climate and the influence this will have on seedling survival.

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